Quaternary International 219 (2010) 145–151

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Persistence of tree taxa in Europe and Quaternary climate changes

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ARTICLE INFO

Article history:
Available online 6 November 2009

ABSTRACT

The possibility that some populations of tree species may have survived multiple Quaternary glacial–interglacial cycles in central Europe is discussed. The alternation of forest and non-forest phases observed in long pollen records shows a substantial correspondence with the variations in global ice volume and indicates that the last glacial has been one of the most unfavourable periods for tree survival in Europe. Therefore the species that have survived the last glacial period in central Europe may have reasonably persisted also during less severe glacial periods and ultimately since the beginning of the Quaternary. The history of *Picea* and *Corylus* exemplifies the possibility of a continuous presence of trees in Europe. Recognizing the persistence of tree populations is necessary to assess the timing of their genetic diversification. The importance of extending the observation of the species behaviour to the time scale of the whole Quaternary is highlighted, in order to explain the modern distribution of populations and species and to reach a better understanding of evolutionary processes.

1. Introduction

In recent years, a considerable amount of work has been carried out to define the distribution of tree taxa during the last glacial period, with two main practical goals, namely possible suggestions for conservation strategies in view of future climate changes (e.g. Willis and Birks, 2006) and a better understanding of evolutionary processes (e.g. Taberlet et al., 1998). In particular, the hypothesis that temperate trees could only survive the full glacial in pockets of environmentally favourable conditions in southern Europe (Bennett et al., 1991; Tzedakis et al., 2002) has gradually shifted to the possibility of much wider distributions, including central Europe (Willis et al., 2000; Birks and Willis, 2008) and even northern Europe (Stewart and Lister, 2001).

Reconstructing the past location of refugial areas for trees in Europe is fundamental to define the relationships between the contraction/fragmentation of the species' ranges and the genetic diversity observed in modern populations. A number of recent papers explain the modern genetic structure of tree populations on the basis of the location of their refuge areas in last glacial period and subsequent postglacial expansion (e.g. Magri et al., 2006; Liepelt et al., 2008; Tollefsrud et al., 2008). However, very little is known on the effects of previous Quaternary interglacial–glacial cycles on the genetic differentiation of plant populations. Bennett and Provan (2008) argue that the fluctuations of the late Quaternary might be better treated as noise than as signal when studying the origin of modern populations and urge to follow the history of tree populations back in time in order to better understand modes and times of lineage splits.

Quaternary palaeobotanists have always paid special attention to define the progression of tree extinctions in Europe (e.g. van der Hammen et al., 1971; Watts, 1988; Willis and Niklas, 2004; Tzedakis et al., 2006; Postigo Mijarra et al., 2009) and to define the climatic causes for such extinctions (Svenning, 2003; Tzedakis et al., 2006; Leroy, 2007; Willis et al., 2007). This is very important for both biostratigraphic and conservation purposes. On the contrary, the persistence of tree taxa throughout the Pleistocene has largely been neglected, as is not especially meaningful for biostratigraphers and does not provide important insights on conservation strategies of endangered species. However, the recognition that at least a small contingent of tree species may have survived many glacials may be important from the evolutionary point of view, as it may help define the time needed for their diversification.

This paper is a first contribution to this question. In particular, attention has been paid to: (1) the possible persistence of tree taxa in Europe during the Quaternary, (2) the timing of the genetic diversification of modern tree populations in Europe.

2. Quaternary long pollen records in Europe

Long continuous pollen records, although rather sparse in Europe and mostly located in southern Europe, may prove very useful to ascertain the possibility of the persistence of tree taxa in

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doi:10.1016/j.quaint.2009.10.032

Europe over a large part of the Quaternary glacial–interglacial cycles, as they record also the vegetation of the glacial phases (Fig. 1).

The long composite pollen sequence of Leffe in northern Italy (only the Fornace Martinelli core is represented in Fig. 1; 45°48′N, 9°53′E; ca. 500 m a.s.l.), spans the time period from the Olduvai Subchron, whose top is dated 1.77 Ma, to Marine Isotope Stage (MIS) 22, around 0.87 Ma (Muttoni et al., 2007). It records a number of tree taxa currently extinct in Europe, including, among others, *Tsuga*, *Cedrus*, *Carya*, *Pterocarya*, and *Eucommia* (Ravazzi and Rossignol Strick, 1995; Ravazzi, 2003; Ravazzi et al., 2009). On the whole, the pollen sequence shows a considerable continuity of forest vegetation. Different tree taxa follow each other in cyclic patterns, starting with warm temperate trees (e.g. *Quercus*, *Eucommia*, *Corylus*, *Carpinus*), followed by warm and moist taxa (*Carya*, *Pterocarya*, *Juglans*), cool-temperate conifers (*Picea*, *Tsuga*, *Cedrus*, *Abies*) and finally short and modest increases of open vegetation (*Artemisia*, Chenopodiaceae, *Ephedra*). The pollen record from Leffe indicates that harsh glacial conditions were never reached in the Italian Prealps during the Early Pleistocene, as only a few moderate peaks of herbaceous vegetation are recorded. A very similar picture emerges from the pollen record of the Lamone Valley in northern Italy (44°17′N, 11°45′E), tentatively correlated to MIS 64-46 (Fusco, 2007).

The comparison of the Leffe and Lamone Valley records with other long Italian Early Pleistocene pollen sequences (e.g. Pietrafitta: Ricciardi, 1961; Santa Lucia: Joannin et al., 2007; Montalbano Jonico: Joannin et al., 2008) indicates that during the cool phases there was a wider diffusion of mountain forests in Northern Italy with respect to Central and Southern Italy, where a more

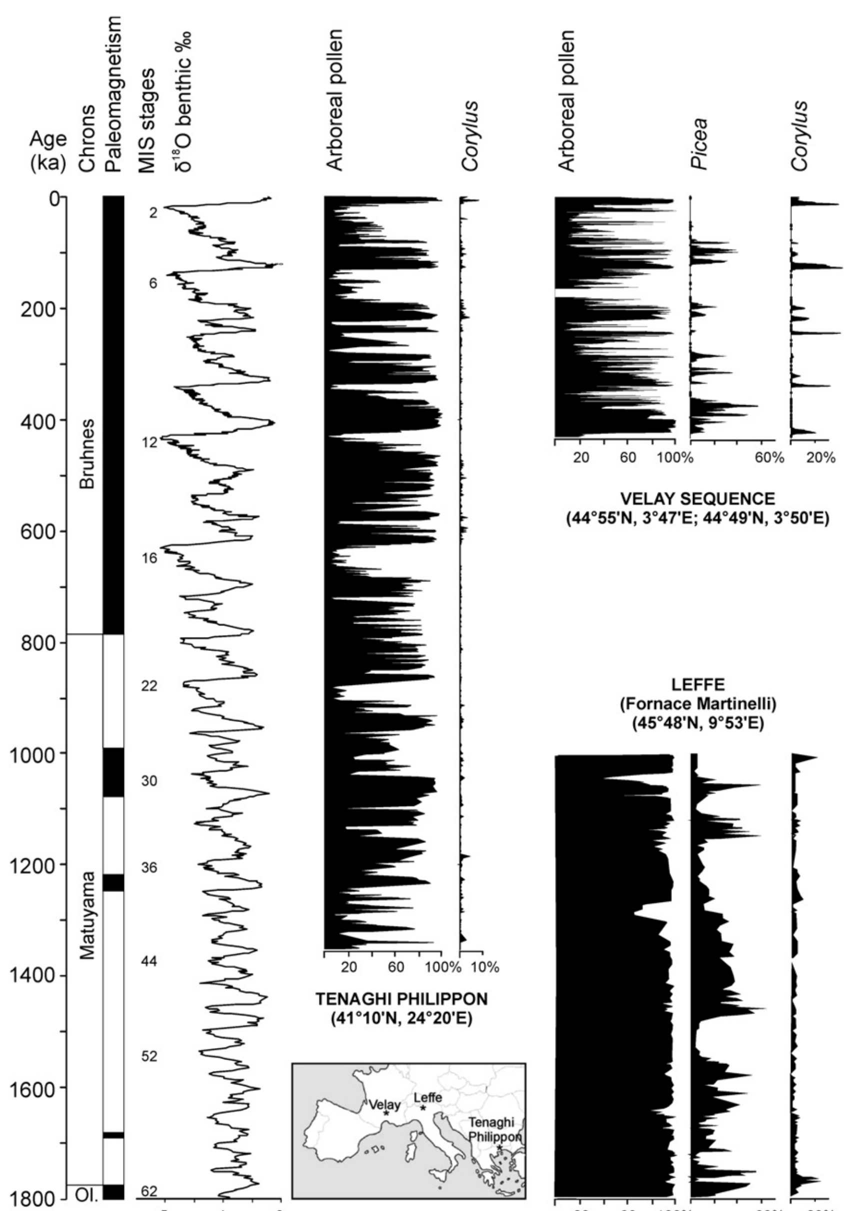

Fig. 1. Summary pollen percentage records from Tenaghi Philippon (redrawn from Tzedakis et al., 2006), the Velay sequence (redrawn from Tzedakis et al., 1997; Reille et al., 2000), and the Fornace Martinelli core from Leffe (redrawn from Ravazzi, 2003; Muttoni et al., 2007). Also shown are variations in $\delta^{18}O$ composition of benthic foraminifera from the LR04 stack of Lisiecki and Raymo (2005) for the last 1.8 Ma. The age of the Tenaghi Philippon record is based on an astronomic calibration of the vegetational phases, revealing a close correspondence between the terrestrial and marine records (Tzedakis et al., 2006), the Velay sequence has been aligned to the marine stratigraphy using glacial-to-deglacial transitions as the tie points (Tzedakis et al., 1997), the Leffe record is not correlated to the marine record. 'Ol.' indicates the Olduvai Subchron.

significant distribution of open vegetation was generally found (Fusco, 2007). However in some southern locations the comparison of marine pollen data with the respective oxygen isotope record reveals that glacial intervals were characterized by alpine forest conditions, whereas a wooded steppe landscape became established at the beginning (Valle di Manche: Capraro et al., 2005) or at the end of the deglaciations (Zakynthos Island: Subally et al., 1999).

The Tenaghi Philippon pollen record in Greece (41°10′N, 24°20′E; 40 m above sea level) spans approximately 1.35 million years and encompasses more than forty interglacial stages, as assessed in the marine isotope stratigraphy (Fig. 1; Wijmstra, 1969; Wijmstra and Smit, 1976; Wijmstra and Groenhart, 1983; Tzedakis et al., 2006). The record shows the progressive local extinction of many taxa, occurring at different times along the core, including *Parthenocissus*, *Liriodendron*, *Tsuga*, *Parrotia*, *Cedrus*, *Carya*, *Pterocarya*, and *Eucommia*. Besides, the record indicates that some tree taxa have a considerable persistence, being always represented in the pollen diagram, except in short intervals corresponding to glacial periods. Such tree taxa, including *Quercus*, *Carpinus*, *Ostrya*, and *Corylus*, were living in the region already during MIS 40, and are still present in southern Europe, as well as in large parts of central Europe. The most severe contractions of tree populations occurred during the glacial maxima of MIS 12, 16, 6, 2, 10 and 8, in descending order of severity (Tzedakis et al., 2006), in agreement with estimated ice volume maxima at MIS 2, 6, 12 and 16, with MIS 12 and 16 showing ice volume greater than at the last glacial maximum (Shackleton, 1987).

The Middle-Late Pleistocene composite pollen diagram from the Velay plateau, including the Lac du Bouchet sequence (44°55′N, 3°47′E; 1200 m a.s.l.) and the Praclaux record, 9 km away (44°49′N, 3°50′E; 1100 m a.s.l.), covers four climatic cycles preceding the Holocene (Fig. 1; Reille and de Beaulieu, 1990, 1995; Reille et al., 1998, 2000). The correlation of the Velay sequence with the discontinuous sedimentary records of central Europe has provided an unique opportunity for advancing a palynostratigraphic framework valid for central Europe (de Beaulieu et al., 2001). This framework is mostly based on the floristic and vegetational features of the interglacial periods, while very little is known about the vegetation of the last glacial periods in central Europe, apart from the Velay pollen sequence. A comprehensive view of this pollen record suggests that a number of taxa may have been always present in the region, although in some levels their pollen is missing. They include arboreal taxa (e.g. *Pinus*, *Picea*, *Juniperus*, *Betula*, *Quercus*, and *Corylus*), as well as non-arboreal taxa (e.g. Poaceae and *Artemisia*) (Reille et al., 2000). The sporadic appearances of tree pollen during the glacial periods, similarly to other pollen sites from southern Europe where trees are believed to have survived the glacials (e.g. Valle di Castiglione: Follieri et al., 1988; Tenaghi Philippon: Wijmstra, 1969; Wijmstra and Smit, 1976) suggests caution in excluding that at least some tree populations may have persisted in the Velay region during the last 400 ka: they may have undergone severe contractions without completely disappearing from the region, so leaving feeble traces of their presence. Within each interglacial, a clear succession of taxa increasing one after the other is observed: in many cases, after a first expansion of *Pinus*, mesophilous taxa appear, usually following the succession *Betula*–*Quercus*–*Corylus*, followed by *Carpinus*–*Abies*–*Fagus*, and finally *Picea* and *Pinus*. However this succession is not a conclusive evidence of migration from distant sites (Tzedakis and Bennett, 1995). In fact a cyclic pattern of tree expansion is observed also in the Early Pleistocene pollen record from Leffe (Ravazzi, 2003), where migration from other regions appears very unlikely. The interglacial succession of tree taxa may be possibly due to climate changes and/or soil development.

Apart from these long pollen sequences, in central and northern Europe several pollen diagrams record single Early and Middle Pleistocene interglacial phases (e.g. de Jong, 1988; Zagwijn, 1992; Urban, 1995; Ber, 2005). The diverse vegetation characters of the interglacials are much more significant than the glacial vegetation features from the biostratigraphical point of view, but are not informative about the possible persistence of trees in the region during the glacial period. Even so, a different pattern of forest development has been observed in different forest phases: interglacial pollen records of Early Pleistocene age from The Netherlands (e.g. Leerdam, 51°90′N) show that temperate trees spread and declined together, while interglacials more recent than 1 Ma display a succession in the appearance and expansion of temperate trees (de Jong, 1988; Zagwijn, 1992).

3. The response of forest vegetation to Quaternary climate changes

The observed different behaviour of forest vegetation in the Early Pleistocene compared to the Middle Pleistocene may be partly due to the different characters of the climatic cycles. In fact, the climate of the Early Pleistocene was dominated by 41-ka cycles, corresponding to obliquity forcing. After about 800 ka BP glacial–interglacial cycles occur with a much longer mean period of approximately 100 ka, corresponding to eccentricity cycles. The increase of the periodicity of glacial–interglacial cycles was accompanied by an increase in the amplitude of global ice volume variations, in part attributable to the prolonging of glacial periods, as clearly shown by high-resolution oxygen isotope data from deep sea cores (cf. the variations in $\delta^{18}O$ composition of benthic foraminifera from the LR04 stack of Lisiecki and Raymo (2005) in Fig. 1). The final effect is an increasing contrast between warm and cold periods, which may be expected to affect also the vegetation history of temperate Europe.

The Tenaghi Philippon record reveals a close correspondence between variations in global ice volume and forest contractions/expansions over the last 1.35 Ma (Tzedakis et al., 2006). The other long European pollen records confirm a general amplification of the glacial/interglacial cycles as recorded by past vegetation changes in the course of the Quaternary. Although located at approximately the same latitude, the Leffe (Ravazzi, 2003) and the Velay records (de Beaulieu et al., 2001) clearly show different patterns of forest development (Fig. 1): low amplitude, high frequency cycles of vegetation dynamics, with very moderate steppe episodes, are found at Leffe in the Early Pleistocene, while high amplitude and low frequency variability are recorded in the Velay diagram, that shows also very pronounced steppe phases during the glacial periods, witnessing an intensification of glaciations. The exiguity of the steppe phases at Leffe cannot be ascribed to a low temporal resolution of the diagram, as it is consistent with other coeval pollen records from Italy showing only modest steppe phases during the Early Pleistocene (Fusco, 2007). By contrast, the Italian records show a considerable expansion of steppe and grasslands during the glacial phases of the Middle and Late Pleistocene (Follieri et al., 1988; Russo Ermolli, 1994). Summarizing, in the Early Pleistocene the open vegetation phases are short compared to the forest phases, while during the Middle-Late Pleistocene long glacial periods alternate with shorter interglacials (Leroy, 2007).

It is common opinion that the chance of losing tree species is maximum during periods with a climate unfavourable for tree survival, which is considered to have occurred during the glacial periods (Leroy, 2007). Svenning (2003) has shown that extinct and relictual tree taxa in Europe are less tolerant of cold growing season and winter temperatures than widespread taxa, and that extinct taxa are less drought tolerant than relictual taxa. Based on these observations, one would expect a lower rate of tree extinctions during the Early Pleistocene, when open vegetation phases were short compared to forest phases, than in the Middle-Late Pleistocene, when glacials have been longer and colder. Surprisingly, the fossil record indicates that most regional extinctions occurred in the Early Pleistocene. Both in northwest Europe and in the Iberian Peninsula the number of taxa that disappeared during the Early Pleistocene doubles the number of the taxa extirpated in the Middle and Late Pleistocene (Willis and Niklas, 2004; Postigo Mijarra et al., 2009). This apparent discrepancy between the progression of regional extinctions of tree taxa and the importance of the Quaternary climate fluctuations probably requires more precise vegetational data of Early and Middle Pleistocene age.

In spite of climate oscillations, a number of tree taxa have apparently persisted since at least the Early Pleistocene somewhere in Europe. The southern European countries are commonly believed to be the refugial areas for trees during the glacial periods and therefore nobody would be surprised that many genera and species have not moved from their Mediterranean locations since the beginning of the Pleistocene and even before (Médail and Diadema, 2009). In fact, a significant number of palaeo-endemic species are known from the Mediterranean regions, resulting from a long-term regional permanence without evolutionary changes (Greuter, 1995; Thompson, 2005; Magri et al., 2007).

In the light of the recent observations that at least some temperate trees may have survived the last glacial at higher latitudes than the Mediterranean regions (Willis et al., 2000; Stewart and Lister, 2001; Magri et al., 2006; Birks and Willis, 2008), the question of the persistence of tree taxa in Europe since the beginning of the Pleistocene may be considered with a wider prospect than simply the Mediterranean Basin. We know from both global ice volume variations (Shackleton, 1987) and pollen records (Tzedakis et al., 2006) that the glacial maxima at MIS 2, 6, 12 and 16 have been the most severe of the whole Pleistocene (Fig. 1). It follows that the tree taxa that survived the last glacial maximum endured one of the climatically most unfavourable periods of the Pleistocene. Therefore, it is reasonable to assume that the tree taxa surviving the last glacial period in central Europe may have persisted during the other more or less equally harsh glacials (MIS 6, 12, and 16) and throughout the previous milder glacial periods. Ultimately, it is possible that tree taxa present in central Europe during the last glacial may have persisted over a large part or the whole of the Pleistocene.

4. Woody taxa persistence during the Quaternary

The history of some woody taxa recorded in Europe from the Early Pleistocene up to the Holocene may exemplify the problem.

Picea is found with continuity in Mediterranean pollen records (e.g. Semaforo-Vrica sections: Combourieu-Nebout and Vergnaud Grazzini, 1991; Saint-Macaire: Leroy et al., 1994; Santa Lucia: Joannin et al., 2007; Leroy, 1997, 2008) and in alpine sites (Fig. 1; Ravazzi, 2003) during the Early Pleistocene. It is also well represented in the Early and Middle Pleistocene interglacial phases in northwest and central Europe (Zagwijn, 1992; Urban, 1995; Ber, 2005; Preusser et al., 2005; Pastre et al., 2007). During the Middle Pleistocene, its presence is documented by pollen and macrofossils in northern Italy (Rossi, 2003; Martinetto, 2009; Pini et al., 2009), while it underwent a strong reduction in Southern Italy (Follieri et al., 1988; Russo Ermolli, 1994; Munno et al., 2001). In the long composite pollen record from the Velay it expanded during the interglacial periods and occurred frequently during the four last glacial periods (Fig. 1). It disappeared during the last glacial maximum and the Holocene (de Beaulieu et al., 2001). Consistently, the modern distribution of *Picea* does not include this part of France. In the British Isles *Picea* pollen occurred in low frequencies throughout the cold stages since the Early Pleistocene, it was a significant member of the first interstadials of the last glacial (Early Devensian), it became rare in the late Devensian and is presently regionally extinct (West, 2000). The continuous record of *Picea* in Britain throughout the Early and Middle Pleistocene is considered to result from long-distance aerial transport and/or reworking (West, 2000), but even so it indicates that spruce was continuously present in neighbouring regions in Europe during the glacial periods and/or during the interglacial periods whose sediments might be reworked in the following glacials. Macrofossil and pollen data testify that *Picea* survived the last glacial maximum at least in the Alps, Slovenia, Carinthia, the Hungarian Plain, and the Carpathians (Ravazzi, 2002; van der Knaap et al., 2005; Latałowa and van der Knaap, 2006), where it is still living today. In addition, pollen data indicate that *Picea*, most likely *Picea abies* subsp. *obovata* still living in northern Europe in regions where permafrost occurs close to the ground surface, survived in the Baltic States and adjacent Russia in northern Europe (Latałowa and van der Knaap, 2006). Based on these data, *Picea* has a real chance to have persisted in central Europe during previous glacial–interglacial cycles, possibly down to the beginning of the Pleistocene, while it underwent a progressive reduction in southern and western Europe.

The possibility of a long-term persistence of woody taxa through many glacial–interglacial cycles in central Europe is not restricted to conifers. *Corylus* appears as another possible candidate (Fig. 1). It survived several glacial–interglacial cycles in the Leffe Basin (Italian Pre-Alps) during the Early Pleistocene (Fig. 1), when it was also found during interglacial phases in northern Europe (Zagwijn, 1992). In Middle Pleistocene interglacials it is found in France (Pastre et al., 2007), Italy (Pini et al., 2009; Martinetto, 2009), Switzerland (Preusser et al., 2005), Poland (Ber, 2005), and Germany (Urban, 1995). During the four last glacial periods, *Corylus* only temporarily disappears in the long pollen record of the Velay (de Beaulieu et al., 2001), where it always shows marked early expansions in the interglacial succession (Fig. 1). In Britain, in addition to a significant diffusion of *Corylus* during the interglacial periods, there are a few records of hazel nuts during the last glacial period and a more widespread *Corylus* pollen record of very low frequencies (usually <2%) in cold stages back to the Early Pleistocene (West, 2000). Although reworking is considered to be the probable source of these records, the continuity of the finds may also suggest a continuous presence of *Corylus* with a very sparse distribution. In central and north-western Europe the hazel expansion often preceded other deciduous trees also at the beginning of the Holocene. Among other hypotheses to explain this pattern, it has been suggested that *Corylus* could rapidly expand from low-density populations in response to a climatic change (Tallantire, 2002). Interestingly, in the Southern Alps, where the glacial survival of *Corylus* is not questioned, its expansion occurred later than in central Europe (Finsinger et al., 2006). Unexpectedly old megafossils finds of *Corylus avellana* from the southern Swedish Scandes, dated to 8700–7000 yr BP, suggest scattered northern refugia in addition to a possible rapid long-distance dispersal (Kullman, 2008). On the whole, these data suggest that, if *Corylus* was not extirpated from central Europe during the last glacial period, one of the most extreme cold phases of the whole Pleistocene, the modern populations of hazel may be the result of a long-term persistence in at least some central European areas.

5. Timing of the genetic diversification of modern tree populations in Europe

Combined genetic and palaeobotanical analyses often show a remarkable correspondence between the location of tree populations during the last glacial period and their modern genetic distribution (e.g. Magri et al., 2006; Liepelt et al., 2008). However the question whether the genetic differentiation of tree populations occurred during the last glacial period or in earlier time-periods has never been really discussed in detail. The data available for European beech suggest that most refuge areas of the last glacial were occupied by *Fagus* also in the previous glacial periods, so suggesting that the modern genetic diversity was not shaped by a single glacial episode but by multiple interglacial–glacial cycles, since at least the middle Pleistocene (Magri et al., 2006). Going back in time the palaeobotanical data are too scanty to reconstruct in detail the location of glacial refugia, so a discussion of the possible age of genetic differentiation of tree populations has seldom been tackled.

In southern Europe, there is evidence that the genetic differentiation of some tree populations of palaeo-endemic taxa may date back to the Tertiary. The distribution of haplotypes of *Quercus suber* and of mitotypes within *Pinus pinaster* populations shows a remarkable conformity with the rifting and dispersion of microplates (Corsica, Sardinia and Kabylie) dating back to the Oligocene, suggesting that for at least 15 Ma these populations have persisted in each terrane without detectable genetic modifications (Magri et al., 2007). The modern genetic structure of these tree taxa appears to reflect the tectonic history of the region rather than Quaternary climate oscillations.

Hampe and Petit (2005, 2007) advance possible explanations for the capacity of some tree species to conserve traces of ancient population dynamics, including longevity and long generation time, as well as geographical persistence. This may result in molecular stasis, especially in regions where the impact of Quaternary climatic oscillations was reduced because of southern location and rugged topography. Hampe and Petit (2007) suggest that similar low rates of evolution might be expected in regions with mediterranean-type climate or in the tropics.

In the light of the possible persistence of tree taxa in central Europe over the Quaternary, as discussed above, the hypothesis of long times of genetic diversification should be considered also for higher latitudes. This may be the case for woody taxa like *Picea* and *Corylus*, as well as for other mesophilous taxa.

The modern genetic data for *P. abies* show a deep divergence between the mitochondrial lineages of the northern range (including northern Poland, Fennoscandia, the Baltic States and European Russia) and of the southern range (including the rest of Europe), indicating that the populations in the two regions were separated for a substantial period of time (Tollefsrud et al., 2008), and supporting the possibility of the persistence of spruce since at least the beginning of the Quaternary. In the northern range a shallow genetic structure is observed, suggesting that the vast northern range was colonized from a single population, while a significant structuring of genetic variation in the southern range of the species indicates the presence of several distinct populations. Tollefsrud et al. (2008) explained the genetic structure and diversity of these southern populations as an effect of isolation during the last glacial maximum and subsequent postglacial colonization. However, some distribution patterns of genetic groups of *Picea* were difficult to explain. A disjunct distribution is observed in the main group of the southern populations: the Alps and the northern Carpathians, occupied by the same genetic group, are separated by a different population living in the Bohemian Massif. Considering that fossil data indicate that these populations may have persisted in central Europe for hundreds of thousands (or even millions) of years, this disjunction may be very old and not ascribable to the last glacial.

Genetic data for *Corylus*, including polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) and microsatellites, show very little genetic variation over Europe (Palmé and Vendramin, 2002). The microsatellite markers allow separating Europe into two areas: a western/northern group containing most of the European populations and a south-eastern group including Italy and the Balkans. These data confirm the existence of glacial refugia in central and western Europe, where a rapid expansion from several scattered refugia appears as a quite possible scenario (Palmé and Vendramin, 2002). A long-term persistence of *Corlyus* in large parts of Europe, as indicated by fossil data, may have produced a high gene flow, resulting in little genetic variation over a large area.

Interestingly, two other broad-leaved tree species, *Carpinus betulus* (Grivet and Petit, 2003) and *Fagus sylvatica* (Magri et al., 2006), show the same geographical structure of *Corylus*, with one single haplotype in western and central Europe and most of the diversity in the Italian and Balkan peninsulas, suggesting a rather diffuse survival in central Europe.

On the whole, these data advise caution in interpreting the modern genetic structure of tree populations in Europe as the result of population contractions and expansions occurred during the last glacial and highlight a much longer temporal perspective, which is still almost completely unexplored.

6. Conclusions

While the progression of tree extinctions in Europe and the climatic causes for such extinctions has been the subject of many studies by European palaeobotanists, the possible persistence of tree taxa over the Quaternary has largely been neglected or discarded. For southern Europe there is acceptance of a continuous presence of thermophilous trees since the Tertiary. The recent recognition of glacial refuge areas for woody taxa in central Europe based on pollen and macrofossil data and the considerable attention paid by geneticists on the consequences of species survival in refuge areas during the glacial periods rise new questions on the history of tree species and their response to Quaternary climate changes, and open a new scenario on possible long-term persistence of trees in central Europe. This possibility is advanced here as an alternative to the common hypothesis of a recent (postglacial) introduction of tree populations in central Europe from the Mediterranean peninsulas.

This paper has shown that long European pollen records have a close correspondence with the Quaternary climatic fluctuations recorded by oxygen isotope data as concerns the frequency and amplitude of glacial–interglacial cycles. A general amplification in forest/non-forest cycles is clearly observed in the course of time, and especially since approximately 800 kyr BP. It clearly appears that the last glacial period has been one of the four most severe of the whole Pleistocene, regarding both ice volume extent and reduction of tree populations. It follows that the studies on the distribution of tree populations during the last glacial period deal with a time interval with exceptional biogeographical features. In the light of this observation, the recognition that populations of tree species may have survived the exceptionally severe last glacial period also at middle latitudes in Europe takes on a great importance because it moves back the history of species to a much longer time scale than the last glacial–interglacial cycle.

The history of two woody taxa has been considered, *Picea* and *Corylus*. The palaeobotanical data indicate that both of them may have been continuously present in central Europe since at least the Early Pleistocene. The modern genetic data are consistent with this scenario.

Finally, this paper clearly shows the importance of extending the observation of the species behaviour to the time scale of the whole Quaternary, if the modern distribution of populations and species is to be explained and evolutionary processes understood.

Acknowledgements

I thank Maria Follieri, Maria Rita Palombo and Igor Parra for useful comments on the manuscript. Maria Bianca Cita, Chronis Tzedakis and an anonymous reviewer are acknowledged for their remarks and suggestions. This work was supported by the projects MIUR Università 2007.C26A07LPWJ and MIUR Università 2008.C26A08WBX5.

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